

series are diverging from the central stock, and the order in which the different changes are achieved. Considered in this manner, the diagram comes a little closer to Lam's (1936) ideal phylogenetic model, in which each detail, dimension or direction should have a definite meaning.

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## DIOECIOUS MELANDRIUM IN WESTERN NORTH AMERICA

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A history of the spread of *Melandrium dioicum* (L.) emend. Coss. and Germ. and *M. album* (Mill.) Garcke following their introduction (with impure clover seed from Europe and in rubbish from grain ships) into eastern North America has been given elsewhere (Baker, 1945, 1948a). A gradual spread westward is indicated, both species becoming more and more common in meadows, fields and waste places and along railroads in the ballast. There is no North American record of either species from a natural habitat, a fact of particular importance in the case of *M. dioicum* which seems ill-adapted for life as a weed (Baker, 1948b). In Europe plants with coloured petals occurring in cultivated land are of hybrid ancestry (involving *M. album*).

The means of introduction renders it likely that the material of "*M. dioicum*" arriving in America was already hybridised and, with the thrusting of the two obligatorily outbreeding forms into similar habitats, further hybridisation must have been an unavoidable consequence. Forms least resembling *M. dioicum* as it is known in Europe may be expected to have been selected. For this reason, now that the champions have become distributed throughout the United States, one would not expect recognisable *M. dioicum* to be found among the weeds of western North America.

The only specimens of "*M. dioicum*" from western North America available in wartime Britain were both collected in

British Columbia (woods just above sea level, Garrow Bay, Vancouver, 28 April 1935, *Whiting and Stewart*, K). They represent a shade form with rounded leaves but their calyces are very reminiscent of those of *M. album*. It was tentatively suggested (Baker, 1945, 1948a) that these plants might represent extreme segregants from the hybrid swarm occupying a habitat similar to that of one of the European parents.

I am indebted to Dr. E. P. Killip and Mr. C. V. Morton of the Smithsonian Institution, Washington, D. C., for the information that there is no specimen of *M. dioicum* from any of the Pacific States in the National Herbarium.

It was the fortunate experience of the author to accompany Drs. Jens Clausen, William Hiesey and Paul Grun on a journey from the laboratories of the Division of Plant Biology of the Carnegie Institution of Washington at Stanford, California, through Oregon and Washington to British Columbia in May and June, 1949. During this excursion it was possible to make observations upon the occurrence of *M. dioicum* and *M. album* in this region and to consult herbarium material.

A collection believed to be the first record of *Melandrium dioicum* naturalised in Western United States was made in Oregon (ca. one mile east of Vista Point, Columbia River Gorge, Multnomah County, 2 June 1949, *Baker 433*, Herbarium of Leeds University). The plants were well established beneath a canopy of softwood and hardwood trees (e.g. *Acer macrophyllum*, *A. circinatum*, *Alnus rhombifolia*, *Cornus Nuttallii*, *Pseudotsuga taxifolia* and *Thuja plicata*) near the roadside amidst a great profusion of herbaceous species and appeared to be reproducing freely by seed. The appearance of the specimens collected indicates little influence of *M. album* in the genotype and one is not given the impression that a woodland type has segregated from a hybrid swarm involving both species but rather of the establishment of *M. dioicum* by separate introduction.

The suspicion was strengthened by the observation of populations of *M. dioicum* in Stanley Park, Vancouver, British Columbia and in West and North Vancouver. In this area, this species appears to be not uncommon in wooded areas, being found both in clearings and wood borders on one hand and in dense shade on the other. Although a number of calyx characters suggests the influence of *M. album*, the general appearance of the populations as a whole suggests that their origin is to be found in a separate introduction from rather impure European stocks of the species rather than by segregation from a champion population which has pushed its way across the continent from eastern North America. In one case, the species was noticed among debris thrown from a house garden in West Vancouver and its original introduction as an ornamental plant seems likely in con-

trast to the manner in which pink-petalled plants became established in eastern North America.

In this connection, it may be of interest to record that *Geranium Robertianum* found growing in Stanley Park was definitely unlike that which is native to eastern North America and closely resembled European woodland material (Baker, 1949). The considerable connection between maritime British Columbia and the British Isles (until recent decades possibly closer than between western and eastern Canada), may indicate the probable source of *Melandrium dioicum* in the Vancouver area.

At the same time it is significant that Robbins, Bellue and Ball (1941) record that plants with rose-coloured petals occur in populations of *M. album* in California. These rare plants are indicators of past hybridisation with *M. dioicum* which cannot have occurred locally. The colonisation of western North America by *M. album*, although probably reinforced by introduction through the Pacific Coast ports, cannot be separated from the westward march of the white campion across North America for there are records of its occurrence from a complete chain of states from the eastern to the western coasts.

Although it is not claimed that these are necessarily the earliest records, herbarium specimens of *M. album* with the following dates have been seen from western North America. Abbreviations of names of herbaria are according to Lanjouw (1939).

CALIFORNIA. Hoopa Valley, Humboldt County, 1901, Mrs. M. H. Manning, as *Silene Hookeri* (UC). OREGON. Sandy shore of North Santiam River, North Santiam Station, Marion County, 1919, J. C. Nelson, as *Lychnis alba* (WTC). WASHINGTON. Near Coupeville, Whidby Island, 1897, N. L. Gardner 43, as "Silene" (WTC). BRITISH COLUMBIA. Coldstream Ranch near Vancouver, 1917, Miss E. M. Warren (K). ALASKA. Sandy beach formation, Cape Nome Roadhouse 14 miles east of Nome, 1937, C. W. Thornton (K). MONTANA. Waste places, altitude 3200 feet, near Missoula, Missoula County, 1921, J. E. Kirkwood 1103 (UC); Lake MacDonald, Glacier National Park, 1921, Mrs. Susan D. McKelvey (K). IDAHO. Roadside south of Moscow, Latah County, in *Agropyron* prairie zone, 1937, R. F. Daubenmire 37490 (WTC).

It was apparent in the study of herbarium specimens that there is considerable confusion between *Melandrium album* and *Silene noctiflora* L. Table 1 shows the more obvious points of distinction for herbarium specimens.

Investigation of the phylogenetic connection between these two very similar species might lead to valuable conclusions regarding the relationship of *Silene*, *Melandrium* and *Lychnis*, between which genera there is considerable inter-fertility. In fact,

TABLE 1

<i>Melandrium album</i>	<i>Silene noctiflora</i>
Dioecious	Hermaphrodite
Calyx nerves without obvious anastomoses; parts without nerves greenish.	Calyx nerves anastomosing prominently; parts without nerves whitish.
Capsule with 10 teeth which stand upright or spread slightly outwards.	Capsule with 6 slightly recurved teeth.
Seeds tawny; surface bluntly tuberculate.	Seeds grey-brown; surface granulate.
Glandular hairs fairly frequent in region of inflorescence.	Glandular hairs very numerous causing marked viscosity.

a consideration of the many characters by which *Melandrium album* differs from *M. dioicum* leads to the surprising revelation that almost every one may be supplied by *Silene noctiflora*! Over one hundred years ago, Gärtner (1849) crossed *Melandrium dioicum* with *Silene noctiflora* and obtained a hybrid in which rather less than a quarter of the capsules contained up to fourteen seeds. The repetition of this cross is, therefore, of very considerable importance and a determined effort to extract a form similar to *M. album* from the products of recombination might well be successful. The evidence from geographic distribution is in harmony with such a suggestion for *Silene noctiflora* is probably of South European origin and it has been shown (Baker, 1945, 1948a) that the centre of distribution of *M. album* is in the Mediterranean region. Also, such an investigation might, once and for all, settle the arguments whether *M. album* and *M. dioicum* are to be considered specifically or merely sub-specifically distinct.

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